

# Ecological and environmental context shape the differential effects of a facilitator in its native and invaded ranges

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**Abstract.** Invasive species often exhibit disproportionately strong negative effects in their introduced range compared to their native range, and much research has been devoted to understanding the role of shared evolutionary history, or lack thereof, in driving these differences. Less studied is whether introduced species, particularly those that are important as facilitators in their native range, have persistent positive effects in their invaded range despite a lack of a shared evolutionary history with the invaded community. Here, we manipulated the density of a habitat-forming facilitator, the high intertidal acorn barnacle *Balanus glandula*, factorially with herbivore density in its native range (Bluestone Point, British Columbia, Canada) and invaded range (Punta Ameghino, Chubut Province, Argentina) to determine how this facilitator differentially affects associated species at these two locations. Given that high intertidal species at Punta Ameghino (PA) are evolutionarily naïve to barnacles, we predicted that the positive effects of *B. glandula* at PA would be absent or weak compared to those at Bluestone Point (BP). However, we found that *B. glandula* had an equally positive effect on herbivore biomass at PA compared to BP, possibly because the moisture-retaining properties of barnacle bed habitats are particularly important in seasonally dry Patagonia. Barnacle presence indirectly decreased ephemeral algal cover at BP by increasing grazer pressure, but barnacles instead facilitated ephemeral algae at PA. In contrast, *B. glandula* increased perennial algal cover at BP, but generally decreased perennial algal cover at PA, likely due to differences in dominant algal morphology. Though our experiment was limited to one location on each continent, our results suggest that shared evolutionary history may not be a prerequisite for strong facilitation to occur, but rather that the nature and strength of novel species interactions are determined by the traits of associated species and the environment in which they occur.

**Key words:** *Balanus glandula*; biogenic habitat; British Columbia; environmental stress; facilitation; foundation species; intertidal zone; invasive species; Patagonia; positive interactions.

## INTRODUCTION

Species introductions are changing the composition and dynamics of ecological communities throughout the world (Ricciardi et al. 2013). Many newly arrived species rapidly become ecological dominants that can have an array of positive and negative impacts on native species. As a result, there has been much interest in how the ecology and traits of a species in its native range predict its impacts in newly invaded areas (Fournier et al. 2019).

Ecologists have long supposed that invaders often have stronger negative impacts in their invaded range

than in their native range (Darwin 1859, Elton 1958). For example, invasive predators may be able to exploit naïve prey in their invaded range (Sih et al. 2010), as happens with snakes or rodents introduced to islands with no similar predators (Wiles et al. 2003, Harper and Bunbury 2015). Novel weapons such as allelopathic chemicals may increase the negative effects of invading species on the recipient community (Callaway et al. 2012). Invaders, released from their natural parasites and consumers, may become competitive dominants in their invaded range (Keogh et al. 2017, Lucero et al. 2019). Further, invasive species may be able to facilitate the establishment of other coevolved introduced species (Simberloff and Von Holle 1999). Despite the growing list of invasion impact case studies conducted in invaded ranges, explicit comparisons of the effects of introduced species between their native and introduced ranges are

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rare (Hierro et al. 2005, Gribben and Byers 2020). Available data suggest that many invaders do have stronger negative effects in their introduced ranges, although the mechanisms behind these observations are not always clear (Callaway et al. 2012, Maurel et al. 2013, Puritty et al. 2018).

Although there are many spectacular examples of their negative impacts, introduced species may also have positive impacts in their recipient community. For example, introduced prey that can be exploited as a dietary resource may bolster native predator abundance (Pintor and Byers 2015), and some introduced generalist pollinators can increase reproductive success in native plants (Agüero et al. 2020). Introduced species may act as ecosystem engineers and provide biogenic habitat for native species, of which there are many examples including bivalves (Gestoso et al. 2013), mangroves (Demopoulos and Smith 2010), mudsnails (Thyrring et al. 2013), seaweeds (Wright et al. 2014), and terrestrial woody plants (Procheş et al. 2008).

While few studies have examined how the positive effects of a facilitator change upon its introduction to a new system, we can still make basic predictions about what might occur. Because introduced species generally have no recent shared evolutionary history with native species in the introduced range, and thus no selection strengthening their association, an introduced facilitator should provide comparatively little benefit to native species (Bronstein 2009). This prediction appears to hold for ectomycorrhizal fungi, which associate with plant taxa in their native range but often cannot associate with evolutionarily naïve plants elsewhere (Vellinga et al. 2009). Many novel facilitations involve generalist facilitators, where the identity of the facilitator is of little importance to the interaction, but these usually form only if a native functional equivalent exists (Aslan et al. 2015). Absent such functional equivalents, we would expect facilitators to have weaker positive effects in their introduced range.

In addition to shared evolutionary history, local environmental context may be a strong driver of facilitation strength, particularly for those interactions that involve a facilitator mitigating environmental stress for associated species. The benefit facilitators provide, and thus the strength of facilitation, is often more pronounced in stressful environments (Bertness and Callaway 1994, Bertness and Leonard 1997, He et al. 2013). Thus, if conditions in the introduced range are more stressful than in the native range, then a novel facilitation could be stronger than analogous interactions in the facilitator's native range.

In this study, we tested the effect of one such facilitator, the acorn barnacle *Balanus glandula* (Darwin 1854), in its native and its invaded range through concurrent field manipulations in British Columbia, Canada (native range) and Chubut Province, Argentina (invaded range). Barnacles are important facilitators in intertidal rocky shore communities around the world. Though acorn

barnacles are often dominant competitors for space (Connell 1961, Dayton 1971), they also provide a prey base for diverse taxa (Connell 1961, Paine 1980) and serve as ecosystem engineers for many species, providing refugia from hydrodynamic and desiccation stress (Harley 2006). Indeed, barnacles have many known facilitative effects: enhanced recruitment of macroalgae by limiting herbivore access (Dungan 1986, Geller 1991); increased recruitment of sessile invertebrates by providing favorable microhabitats (Menge 1976, Navarrete and Castilla 1990, Bertness et al. 2006); and enhanced density and diversity of mobile species by providing refugia, feeding areas, or both (Harley 2006, Harley and O'Riley 2011).

Historically, there were no mid or high intertidal barnacles along the Atlantic coast of Patagonia (with the exception of Tierra del Fuego, where some chthamalid barnacles are found). However, in the late 1960s, *B. glandula* arrived in Argentina from the west coast of North America. As of 2004, *B. glandula* had spread from its initial foothold in Mar del Plata (a latitude of 38.0500° S) to Cabo Peña in Tierra del Fuego (a latitude of 53.3008° S; Schwindt 2007). This stretch of the Patagonian coast is known for its desiccation stress (Bertness et al. 2006, Silliman et al. 2011) and presents a unique opportunity to study the effects of an ecosystem engineer that has been introduced into a new range, which may weaken facilitation, where there is a considerable level of environmental stress, which may strengthen facilitation.

Because Argentinian high intertidal species are evolutionarily naïve to acorn barnacles, we hypothesized that, even in Patagonia's desiccating environment, the facilitative effects of *B. glandula* would be weaker in their invaded range compared to their native range. To test this hypothesis, we conducted barnacle density manipulations at both Bluestone Point in Barkley Sound, Canada (BP) and Punta Ameghino in the Nuevo Gulf, Argentina (PA) and documented the effects of *B. glandula* on both high intertidal communities. Additionally, we factorially manipulated densities of locally dominant herbivores (true limpets *Lottia* spp. at BP and the pulmonate limpet *Siphonaria lessonii* at PA). First, we predicted that barnacles would facilitate mobile grazers at BP by providing refugia from abiotic stress, but that this facilitation would be absent at PA, where *S. lessonii* has no shared evolutionary history with barnacle beds. Second, we predicted that *B. glandula* would facilitate macroalgae at BP by providing a refuge from herbivory, but would have a more neutral or perhaps negative effect on macroalgae at PA.

## MATERIALS AND METHODS

### Field sites

This research was conducted within the native range of *B. glandula* in British Columbia, Canada from June 2006 to July 2007, and within its invaded range in Chubut Province, Argentina from December 2005 to

February 2007 (Appendix S1: Fig. S1). Due to logistical constraints, experimental manipulations were only conducted at one location on each continent.

Research in Canada was conducted on the traditional territories of the Huu-ay-aht First Nations at Bluestone Point (48.8195° N, 125.1463° W) near Bamfield in Barkley Sound. Bluestone Point (BP) is a semi-exposed granitic shore. Tides are mixed semi-diurnal, with a range of approximately 4 m. Conditions are frequently overcast, temperatures are consistently mild, and relative humidity is generally high year-round. Dominant high intertidal grazers include limpets (mostly *Lottia digitalis*) and littorine snails (*Littorina* spp.). Ephemeral algae—*Ulva* sp., *Urospora* sp., *Pyropia* spp., and occasionally filamentous diatom mats—can also be found, particularly in the winter and/or where grazers are rare. Several species of perennial algae co-occur with *B. glandula* with *Fucus distichus* being the most common, and *Mastocarpus* sp., *Pelvetiopsis limitata*, and *Endocladia muricata* occurring in lower abundance.

Experimental manipulations in Argentina were conducted at Punta Ameghino (42.6185° S, 64.8643° W) in the Nuevo Gulf, a large bay in Northern Patagonia. Punta Ameghino (PA) is a semi-protected mudstone shore. Tides are semi-diurnal with a range of nearly 6 m. Temperatures in this region are generally mild year-round, but desiccation stress occurs seasonally due to exceptionally strong, dry southern trade winds, low precipitation, and low humidity (Bertness et al. 2006, Silliman et al. 2011, Livore et al. 2018). Prior to the arrival of *B. glandula*, there was no native high intertidal barnacle on Argentinian shores beyond the far southern coast (Schwindt 2007). Space occupancy in the high intertidal zone was historically relatively low during the summer, with pulmonate limpets (*Siphonaria lessonii*) being the most common invertebrate above mid-intertidal mussel beds. Additional grazers are largely absent in the high intertidal zone (E. Schwindt, *personal observation*). A suite of ephemeral algae including *Blidingia minima*, *Bangia fuscopurpurea*, *Pyropia columbina*, *Polysiphonia* spp., and *Dictyota dichotoma* appear during the winter (Raffo et al. 2014). *Ralfsia* sp., a non-calcareous encrusting brown alga that grows directly on rock, is the sole perennial macroalga found in the high intertidal zone (Savoya 2006).

#### Characterization of abiotic stress

High intertidal substratum temperature was measured at hourly intervals using iButton temperature loggers for one summer at each location (DS1921G-F5# Thermochron, Dallas Semiconductor, Dallas, TX, USA) following similar methods to those of Harley and Lopez (2003). Briefly, iButtons were wrapped in Parafilm and epoxied (Sea Goin' Poxxy Putty, Permalite Plastics, Rancho Domingo, CA, USA) into pre-chiseled depressions in the rock such that the epoxy surface was flush with the surrounding rock surface. Fine sand from a beach adjacent to each site was pressed onto the surface of the

epoxy before it set to better approximate the characteristics of the natural rock. Substratum temperatures recorded in this way are highly correlated with *B. glandula* body temperature, more so than air temperature (Harley and Lopez 2003).

Monthly relative humidity data were collected for a representative 5-yr period (2015–2020) from weather stations near each study location to approximate local conditions: Tofino, Canada in the native range (Climate Canada) and Puerto Madryn, Argentina in the invaded range (CENPAT Laboratorio de Climatología). This period was used because comparable data for both sites were not available during the experimental period.

#### Experimental manipulations

To distinguish the direct and indirect effects of barnacles on other species, we factorially manipulated barnacle and dominant grazer densities (Appendix S1: Fig. S2). A total of 36 plots (two barnacle treatments × three grazer treatments × six replicates) were established at both PA and BP. In all cases, plots were located on gently sloping surfaces to improve drainage. At PA, the topography of the high intertidal zone was relatively homogenous, allowing us to assign plots to treatments using a stratified random design. At BP, however, local topographic complexity necessitated a blocked design, where all six treatments were replicated once in each of six blocks. Plots within blocks were separated by <2 m, and blocks were 10–50 m apart.

Barnacle treatments consisted of either natural *B. glandula* densities (69.9% ± 3.3% cover at BP, 45.7% ± 2.3% at PA, means ± SE,  $n = 18$ ) or complete removal of barnacles by careful extraction with scrapers, leaving other sessile taxa undisturbed. There were three grazer treatments: an unfenced control treatment; an inclusion treatment, where *Lottia digitalis* at BP and *S. lessonii* at PA were fenced in at natural densities (5.19 individuals per 100 cm<sup>2</sup> in BC, 6.02 individuals per 100 cm<sup>2</sup> at PA); and an exclusion treatment with the same grazers fenced out. Fences were constructed from metallic copper rings (height = 2.5 cm, diameter = 10.7 cm, internal area = 90 cm<sup>2</sup>) and attached to the substratum with epoxy (Sea Goin' Poxxy Putty, Permalite Plastics). This design is demonstrably effective for controlling limpet densities on rocky shores (Harley 2002). When plots were inspected every 4–8 weeks, *Lottia digitalis* and *S. lessonii* were removed when found in the exclusion treatment and added to the inclusion treatment when densities dropped to one or fewer, though both events were rare. An explicit procedural control, in the form of either a coated or partial copper fence, was not used because these constitute partial treatments (Johnson 1992); instead, the control and inclusion grazer treatments were compared to discern if methodological artifacts were present.

Both experiments were initiated at the beginning of the summer in their respective hemispheres: 3 December

2005 at PA, and 15 June 2006 at BP. The experiments were sampled 9–10 times over the following 14–15 months (early summer in year one through mid–late summer in year two). In control plots across all grazer treatments, limpets or pulmonate limpets and littorine snails (BP only) were counted. The percent cover of ephemeral and perennial algal species was visually estimated with the aid of a small quadrat. Finally, barnacle recruits (defined as individuals <2 mm), both *B. glandula* and *Chthamalus dalli* (BP only), were counted. Because young *B. glandula* typically grow beyond this size faster than the intervening time between our sampling dates (Sanford and Menge 2001), we likely undersampled recruits, but by the same token we were unlikely to double count individuals as recruits.

Because experimental plots at BP contained littorine snails, but no equivalent existed at PA, we converted herbivore abundances in unfenced control plots to total herbivore biomass to allow comparison between sites (see Appendix S1 and Fig. S3 for methodological details).

#### Statistical analyses

All analyses were completed using R version 4.0.2 (R Core Team 2020). We modeled temperature and humidity data using linear models with location as the sole fixed effect and modeled all biological response data using generalized linear mixed models with the glmmTMB package (Brooks et al. 2017). To model each biological response variable, we first created full models with the maximum possible level of interaction between fixed effects (grazer treatment, barnacle treatment, time since experiment start, and location if applicable) and a random effect of block nested within location. Removing the random block effect always increased the Akaike information criterion (AIC) and thus it was always included. Model diagnostics (residuals plots and Durbin-Watson tests) were run using the DHARMA package (Hartig 2020). No temporal autocorrelation was detected, and so no random effects for time were included. A dispersion formula was included for models of herbivore biomass, perennial algal cover, and barnacle recruit abundance, which had heteroscedastic residuals. Due to substantive non-linearity in algal cover through time, we chose only three time points to analyze using linear modeling, those closest to the spring equinox and both fall equinoxes at each location. Models of herbivore and barnacle recruit abundance were fit using a negative binomial error distribution. Herbivore biomass, ephemeral algal cover, and cover of *F. distichus* were analyzed using a Tweedie error distribution, while perennial algal cover was logit-transformed and fit using a Gaussian error distribution. Full models were reduced according to AIC and term significance with the drop1 function, and final models were analyzed by Type II ANOVA/ANCOVA using the car package (Fox and Weisburg 2019) with a significance threshold of  $P < 0.05$ . See Appendix S2 for model summaries and

statistical outputs. We acknowledge that by replicating our experiment at only one site within each of the native and invaded ranges of *B. glandula*, we are pseudoreplicating at a biogeographic scale, which may limit the generality of our results beyond these two specific geographic locations.

## RESULTS

### Abiotic conditions

Stress landscapes differed between the two study locations. High intertidal substratum temperatures at BP were more stressful than at PA (Fig. 1). The average daily maximum temperature was 3.4°C higher at BP than PA ( $F_{1,13} = 10.3$ ,  $P = 0.00684$ , Fig. 1b). The upper 99th quantile of temperature was 3.9°C higher at BP than at PA ( $F_{1,13} = 9.30$ ,  $P = 0.00930$ , Fig. 1c). Relative humidity, however, was 35% lower in the Nuevo Gulf than on the west coast of BC near Barkley Sound ( $F_{1,118} = 1158$ ,  $P < 0.001$ , Fig. 1d).

### Herbivore response to barnacles

*Littorina* spp. abundance (Fig. 2a) was high and declined slowly over time in plots containing *B. glandula* but was consistently very low through time where *B. glandula* was absent (barnacles  $\times$  time,  $\chi^2 = 9.379$ ,  $df = 1$ ,  $P = 0.00219$ ). The positive effect of *B. glandula* on *Littorina* spp. was especially strong where limpets were excluded (barnacles  $\times$  grazers,  $\chi^2 = 23.45$ ,  $df = 2$ ,  $P < 0.001$ ). *Lottia digitalis* abundance at BP (Fig. 2b) was higher where barnacles were present ( $\chi^2 = 25.83$ ,  $df = 1$ ,  $P < 0.001$ ) and declined with time ( $\chi^2 = 9.092$ ,  $df = 1$ ,  $P = 0.00257$ ). At PA, *S. lessonii* abundance increased over time where barnacles were present and declined where barnacles were absent (barnacles  $\times$  time,  $\chi^2 = 9.295$ ,  $df = 1$ ,  $P = 0.00230$ ). *Siphonaria lessonii* recruitment at PA was extremely low over the course of the entire experiment (Appendix S1: Fig. S4). While herbivore biomass generally declined over time, this occurred to a lesser extent at PA compared to BP (location  $\times$  time,  $\chi^2 = 3.857$ ,  $df = 1$ ,  $P = 0.0495$ ). Barnacles had a positive, highly significant effect on herbivore biomass at both sites ( $\chi^2 = 137.7$ ,  $df = 1$ ,  $P < 0.001$ ; Fig. 2c).

### Algal cover

The presence of barnacles differentially affected ephemeral algae between sites (Fig. 3). Barnacles at BP reduced ephemeral algal cover, while barnacles at PA increased ephemeral cover (location  $\times$  barnacles,  $\chi^2 = 10.22$ ,  $df = 1$ ,  $P = 0.00139$ ). Where grazers were present (in both the herbivore inclusion and unfenced control treatments), ephemeral algal cover was lower than where grazers were excluded, but this difference was significantly more pronounced at BP than PA

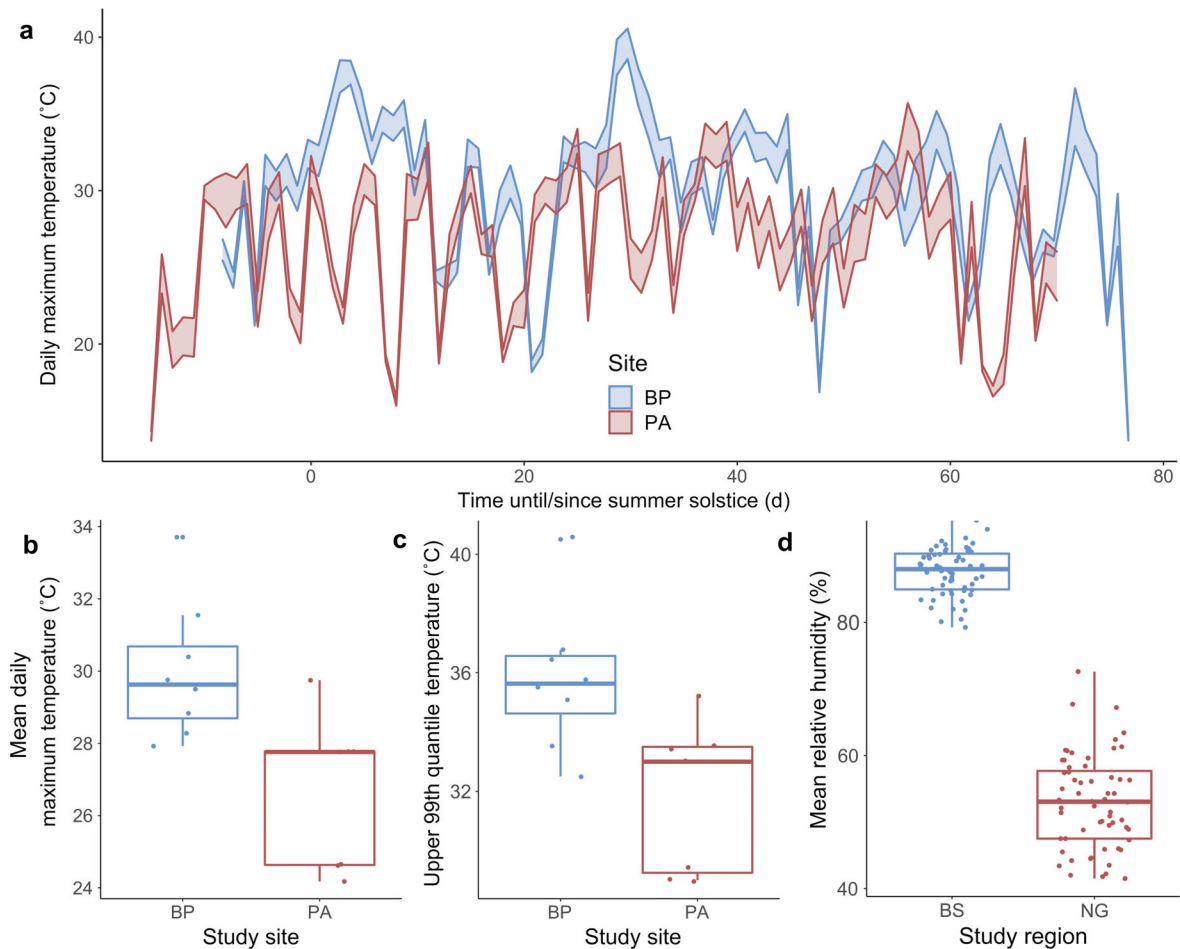


FIG. 1. Abiotic characteristics of study sites at BP (native range) and PA (invaded range). (a) Average maximum daily temperatures recorded by intertidal iButtons during the first summer at each site, a proxy for invertebrate body temperature. Ribbon width represents standard error. Time is relative to summer solstice in each hemisphere (time = 0). (b) Mean daily maximum temperature recorded during the same period. (c) Upper 99th quantile of temperature recorded during the same period. (d) Mean relative humidity recorded in Tofino, British Columbia, Canada (60 km north of Barkley Sound, British Columbia, Canada, BS) and near PA (Nuevo Gulf, Argentina, NG) from January 2015 to January 2020.

(location  $\times$  grazer,  $\chi^2 = 20.98$ ,  $df = 2$ ,  $P < 0.001$ ). Ephemeral algal cover declined slightly over time for the sampling dates analyzed ( $\chi^2 = 7.012$ ,  $df = 1$ ,  $P = 0.00806$ ).

Perennial algal cover (Fig. 4; see Appendix S1: Fig. S5 for logit-transformed data and Appendix S1: Fig. S6 for BP dominant *Fucus distichus*) at BP increased over time in plots with barnacles but remained consistently low where barnacles were absent. At PA, perennial cover tended to decline slightly over time in plots with barnacles present, though this effect was less clear (time  $\times$  barnacles  $\times$  location,  $\chi^2 = 8.641$ ,  $df = 1$ ,  $P = 0.00329$ ). The presence of grazers had little effect on perennial algal cover at BP, but at PA, cover was significantly greater where grazers were excluded (location  $\times$  grazers,  $\chi^2 = 121.9$ ,  $df = 2$ ,  $P < 0.001$ ).

#### Barnacle recruitment

Herbivores reduced the recruitment of *B. glandula*, but this effect was only evident when recruitment was the greatest: at BP during late spring in the second year (location  $\times$  grazers  $\times$  time,  $\chi^2 = 26.32$ ,  $df = 2$ ,  $P < 0.001$ ; Fig. 5). The presence of barnacles increased *B. glandula* recruitment at BP over time, but no such effect was detected at PA (location  $\times$  barnacles  $\times$  time,  $\chi^2 = 4.771$ ,  $df = 1$ ,  $P = 0.0289$ ). The recruitment of a second barnacle species at BP, *Chthamalus dalli*, varied significantly through time, was highest in unfenced plots and generally lowest in grazer exclusion plots, and the effect of herbivores depended weakly on *B. glandula* presence (Appendix S1: Fig. S7; Appendix S2: Table S12).

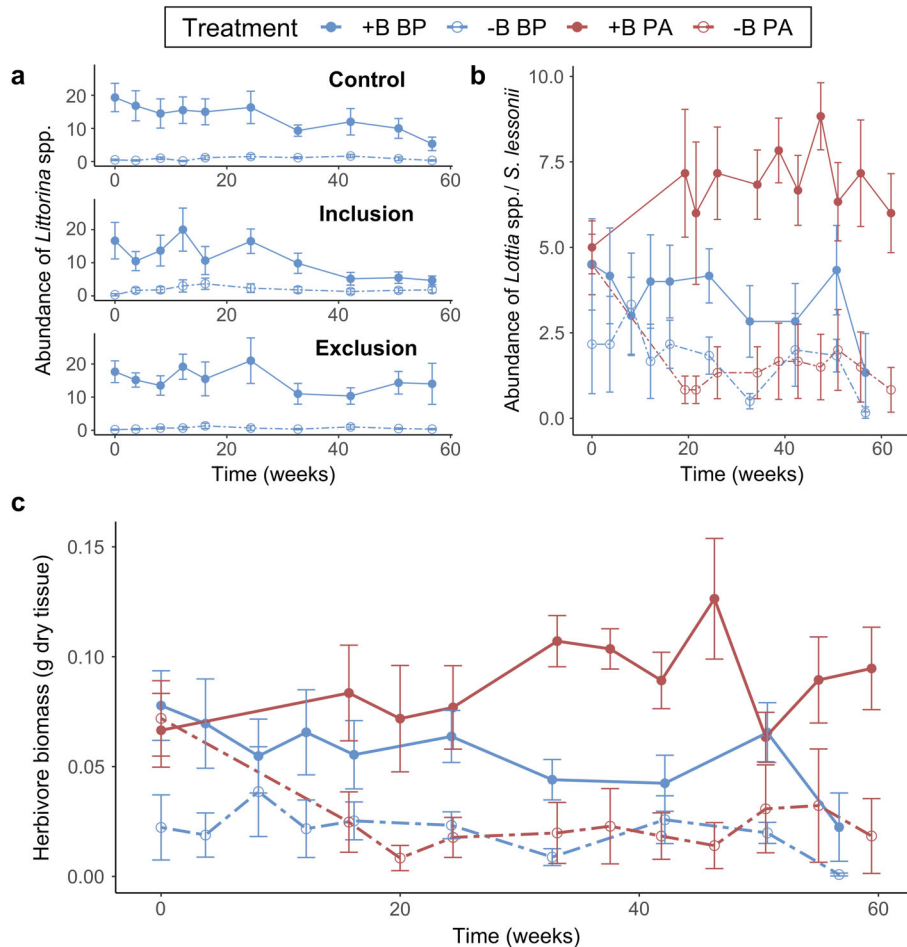


FIG. 2. Change in herbivore abundance over time across treatments (+B, barnacles present; –B, barnacles removed) and sites. (a) *Littorina* spp. abundance at BP, separated into the control, exclusion, and inclusion grazer treatments. (b) Abundance of true limpets (*Lottia digitalis* at BP in blue) and pulmonate limpets (*Siphonaria lessonii* at PA in red) in unfenced grazer control treatments only. (c) Estimated biomass (dry tissue mass) of herbivores in experimental plots. Error bars represent standard error.

## DISCUSSION

Through this experiment, we sought to determine how the ecological effects of the acorn barnacle *Balanus glandula* differed between its native range (west coast of Canada) and invaded range (Argentina), and what mechanisms might drive these differences. We hypothesized that the absence of shared evolutionary history between *B. glandula* and co-occurring species at PA would result in weaker facilitative interactions at PA compared to BP. We predicted that at BP, herbivores and algae would be facilitated by barnacles, which can act as refugia from abiotic and grazing stress. At PA, we predicted that *B. glandula* would not facilitate other species and may instead have a neutral or negative effect on herbivores and algae via competition for space.

Our predictions were only partially supported by our results (see Fig. 6 for a summary of interspecific interactions in both hemispheres). At BP, our results

corresponded well with our expectations and with results from studies conducted at other locations in the native range (e.g., Farrell 1991, Harley 2006); *B. glandula* led to increased herbivore biomass, perennial algal cover, and barnacle recruitment. Ephemeral algal cover was reduced by *B. glandula*, particularly when limpets were excluded; similar results have been demonstrated elsewhere in the native range (Harley 2006, Whalen et al. 2016). In the invaded range, we found that while *B. glandula* suppressed perennial algae overall, this effect was relatively weak and inconsistent across grazer treatments and sampling dates. Surprisingly, *B. glandula* did not substantially affect its own recruitment success at PA. Also unexpectedly, the presence of *B. glandula* at PA increased herbivore biomass to a similar extent as at BP and increased ephemeral algal cover. These observations indicate that *B. glandula* has a range of effects on associated species at these two representative locations within its native and invaded ranges and that facilitation

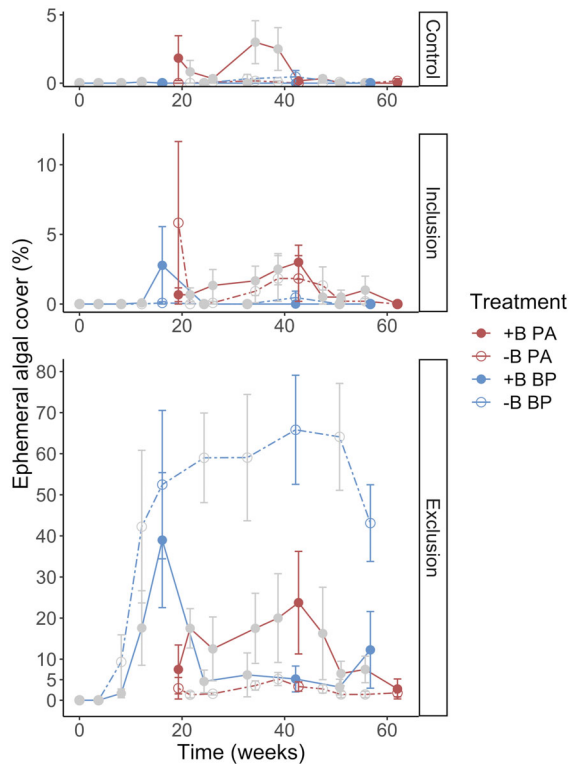


FIG. 3. Percent cover of ephemeral algae within experimental plots over time, separated by grazer treatment (+B, barnacles present; -B, barnacles removed). Note that the  $y$ -axis limits vary between panels. Only data for the time points nearest fall and spring equinoxes were used for analyses; all points excluded from analysis are light gray. Error bars represent standard error. Data for the initial PA survey are not shown due to spurious inflation of algal cover in the -B treatment; an ephemeral microalga was exposed when *B. glandula* was removed, but this alga was only observed at the initial time point.

occurred in the invaded range despite a lack of shared evolutionary history with co-occurring species.

One way that *B. glandula* facilitates associated species is by providing refugia from abiotic stress and grazing pressure (Geller 1991, Harley and O'Riley 2011). For example, upright, foliose fucoids have greater recruitment success in barnacle beds, where desiccation stress and grazing accessibility are reduced relative to bare rock (Farrell 1991). Conversely, encrusting perennial algae settle and grow well on bare substratum due to their higher tolerance of abiotic stress and grazing pressure than upright species (Menge et al. 1983, Steneck and Dethier 1994), and thus may compete with barnacles for primary substratum. The extent to which perennial algae benefit from barnacle refugia is thus largely dependent upon algal morphology. The dominant alga at BP, *Fucus distichus*, is a foliose upright and may thus be more susceptible to grazing and abiotic stress, particularly during the germling and juvenile stages; barnacles provide refugia from these stressors, leading to the

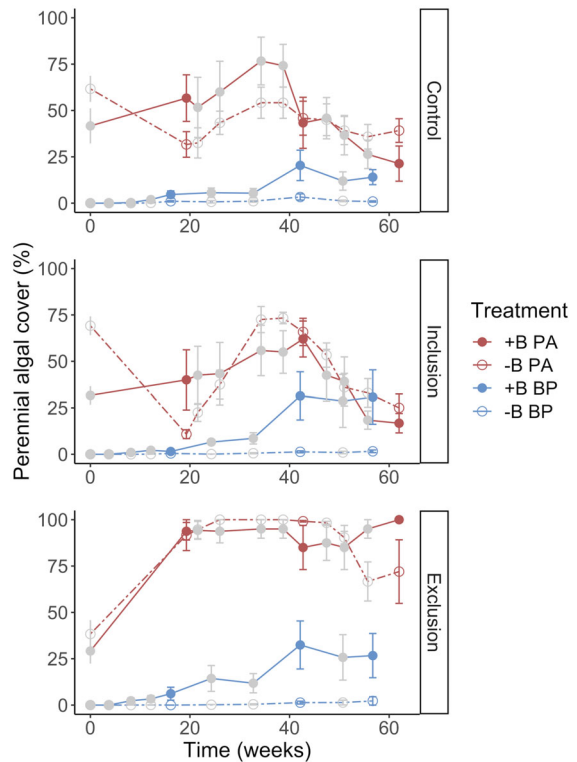


FIG. 4. Percent cover of perennial algae within experimental plots over time, separated by grazer treatment (+B, barnacles present; -B, barnacles removed). Only data for the time points nearest fall and spring equinoxes were used for analyses; all points excluded from analysis are light gray. Error bars represent standard error.

positive association between *B. glandula* and perennial algal cover at BP. The dominant perennial alga at PA, encrusting *Ralfsia* sp., is tolerant to local desiccation stress (Raffo et al. 2014) and although our results show it to be vulnerable to grazing, the presence of barnacles did not mitigate this vulnerability. *Balanus glandula* does not seem to provide refuge from grazing, probably because *Ralfsia* sp. only encrusts bare rock, not barnacle tests. The apparent use of *Ralfsia* sp. as a food source documented here contrasts with the diet of congeners at other locations (Godoy and Moreno 1989), but may result from the limited algal diversity in this particular system (Díaz et al. 2002), or the inadvertent removal of *Ralfsia* sp. and underlying mudstone as *S. lessonii* browses for more palatable microalgae (Craig et al. 1969). Since *S. lessonii* at PA was positively associated with barnacles, and given their removal of *Ralfsia* sp., a negative effect of barnacles on perennial algae may occur indirectly via increased grazing pressure. By the end of the experiment, this trend seemed apparent, but given the complex changes in algal cover over time, a significant interaction of grazer and barnacle treatment could not be resolved.

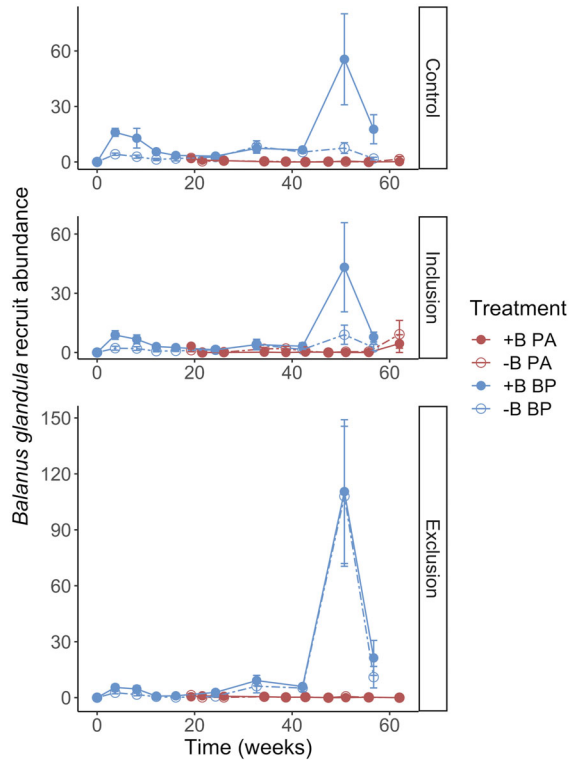


FIG. 5. Density of *B. glandula* recruits over time, separated by grazer treatment (+B, barnacles present; -B, barnacles removed). Note the difference in y-axis limits vary between panels. Error bars represent standard error.

Whether *B. glandula* facilitates ephemeral algae seems contingent upon the extent to which grazing is hindered by barnacles. Ephemeral algae readily colonize bare shores (Viejo et al. 2008) and may be expected to compete with *B. glandula* for substratum. However, ephemeral algae are more palatable than perennial algae and may thus experience greater grazing pressure (Alestra and Schiel 2014). While barnacles can reduce the efficiency of limpet-like herbivores that prefer grazing on smooth surfaces (Creese 1982, Geller 1991), intact barnacle beds and empty barnacle tests can facilitate other mobile grazers (Harley 2006, Sueiro et al 2011). For example, limpet and littorinid snail abundances are usually greater when barnacles are present (Creese 1982, Qian and Liu 1990), a finding consistent with our results at both study sites. Unexpectedly, herbivore abundances declined over the course of the experiment, which appears to be primarily occurring at BP; littorine snail populations can have large temporal variability in recruitment and mortality (Chow 1989), while *L. digitalis* spawning, and thus settlement, may vary substantially depending on patterns of downwelling and upwelling (Shanks 1998), so this trend at BP may be an artifact of beginning the experiment after a period of high recruitment.

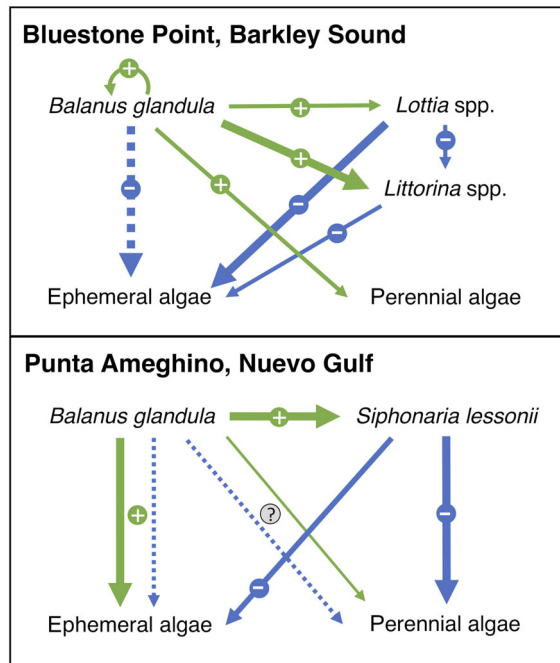


FIG. 6. Species interaction diagrams for the native range of *B. glandula* in Barkley Sound, Canada (top) and the invaded range in the Nuevo Gulf, Argentina (bottom). Green and blue represent positive and negative interactions, respectively. Solid and dashed lines represent direct and indirect effects, respectively. Arrow weight represents the relative strength of interactions.

Grazing pressure was greater in the native vs. the invaded range. While true and pulmonate limpets significantly suppressed ephemeral algal cover at both locations, their effect was greater at BP. When barnacles were present at BP, grazing pressure on ephemeral algae was substantial even in the grazer exclusion treatment due to the presence of barnacle-associated littorine snails. Herbivores in the native range of *B. glandula* have long associated with barnacles: littorine snails and other mesograzers are adapted to use barnacle beds as habitat, while native limpets may be better adapted to graze over barnacles. Because barnacles facilitate herbivores at BP, they also increase grazing pressure and indirectly reduce the cover of ephemeral algae. At PA, *B. glandula* may instead provide a grazing refuge for palatable ephemeral algae from evolutionarily naïve grazers, producing the observed positive effect of barnacles on ephemeral algal cover.

In addition to differences in species traits, differences in environmental stress may have influenced the strength of facilitative interactions between sites. The strength of facilitation may increase with ambient environmental stress (Bertness and Callaway 1994). In this study, ephemeral algae at PA were facilitated by barnacles. While this trend can be explained by differences in the



ecology and traits of species between locations, the local environment may also be important. Temperature stress was slightly higher at BP, potentially due to differences in the thermal capacities of granite and mudstone, the dominant rock type at BP and PA, respectively (Coombes 2011), but PA has substantially lower humidity due to seasonal desiccation stress (Bertness et al. 2006). Desiccation stress negatively affects the germination rate, development, and survival of algal spores and recruits of various species (reviewed in Vadas et al. 1992). Barnacles retain moisture and, in a desiccating environment like PA, facilitation by *B. glandula* may more substantially enhance the survival and performance of algal recruits than in a humid environment such as BP (Mendez et al. 2015).

Patterns of barnacle recruitment also differed between sites. Barnacles, including *B. glandula*, are notoriously gregarious, preferentially settling near other barnacles to allow for sexual reproduction (Wu 1981). This behavior was evident at BP but not PA. Barnacle recruits can be inadvertently removed by limpet grazers as they feed (Dayton 1971), which was observed at BP during peak recruitment in treatments where *L. digitalis* was present, but was not seen at PA. Recruitment patterns seen at BP may have been undetectable at PA due to low barnacle larval density in the zooplankton in this particular region (Menéndez et al. 2011).

Facilitation occurred at PA despite the lack of shared evolutionary history between high intertidal native species and *B. glandula*, which may be due to the generalist nature of this facilitation. Most documented novel facilitations are generalist in nature, particularly when the interaction has only recently been established (Aslan et al. 2015). For example, tube-dwelling polychaetes on mudflats can form mutualisms with an invasive alga just as they do with rare native macroalgae, providing favorable substratum to the alga, which in turn attracts amphipod prey for the polychaetes (Kollars et al. 2016). A novel mutualism with the invasive alga may form only because there are functionally similar native species in the system. Similarly, even though Argentinian species are evolutionarily naïve to *B. glandula*, they could already have the behavioral adaptations needed to utilize barnacle bed habitats if there are functionally equivalent precedents in the system. At PA, these precedents could include native cordgrass (Sueiro et al. 2011) and mussel beds (Bagur et al. 2016) or crevices and holes naturally present in bedrock (Bazterrica et al. 2007, Bagur et al. 2019), all of which increase physical complexity, retain moisture, and/or increase food supply where they are present. *S. lessonii* commonly associates with these features, and thus may have pre-evolved behaviors that drive its association with invasive barnacles. *Balanus glandula* may assuage desiccation stress to directly reduce *S. lessonii* mortality or indirectly increase the presence of algal food for grazers. The latter possibility is supported by the increase in ephemeral algae at PA in the presence of barnacles. We also note that limpet

removal at BP resulted in a disproportionately strong competitive release of *Littorina* sp. in plots containing barnacles, which could reflect barnacle enhancement of microalgae as a result of greater available surface area and/or suitable microhabitats within plots. Regardless, either food enhancement or desiccation reduction could produce the observed positive effect of *B. glandula* on grazers at PA.

Overall, we found that while shared evolutionary history may play a role in determining the strength of facilitation, other factors were more important in driving interactions at the two locations studied. *Balanus glandula* facilitated herbivores at PA and BP; this positive interaction likely occurred because barnacles ameliorate local desiccation stress to enhance survival of associated species, including the algal resource base. *Siphonaria lessonii*, while it has no prior evolutionary experience with barnacles specifically, has encountered topographically similar structures, biogenic or otherwise, in its native range, which could favor an association with *B. glandula*. The morphology of the dominant perennial alga at each site determined whether perennial algae as a whole were facilitated by *B. glandula*. While *B. glandula* provides a refuge from limpet-like herbivores, littorine snails at BP use barnacle beds as habitat, thereby increasing grazing pressure for ephemeral algae attached to barnacles at BP. No analogous species exist in the high intertidal zone of Patagonia, so barnacles instead facilitated ephemeral algae by providing a moist microhabitat that enhanced settlement, survival, or growth regardless of grazer presence. Finally, the type and degree of environmental stress can also shape facilitative interactions: seasonal desiccation stress present at PA may have strengthened facilitation. Our results demonstrate the complex nature of predicting the effects of invasive species. Additional replication of this experiment at other locations within the native and, crucially, the invaded range of *B. glandula* would establish whether our results can be more broadly generalized for this system. More studies that explicitly compare the effects of other introduced species between their native and introduced ranges are needed to explore the relative importance of ecological, environmental, and evolutionary context in shaping novel facilitations.

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#### SUPPORTING INFORMATION

Additional supporting information may be found in the online version of this article at <http://onlinelibrary.wiley.com/doi/10.1002/ecy.3478/supinfo>

#### OPEN RESEARCH

All data, both raw and clean, along with code and metadata (Hesketh et al. 2021) are available in Figshare: <https://doi.org/10.6084/m9.figshare.14675361>. A reproducible R project with associated data and scripts is accessible through Github and archived on Zenodo: <https://doi.org/10.5281/zenodo.4792517>.